A preliminary phylogenetic analysis
of Australian Triaenonychidae (Arachnida: Opiliones)

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A preliminary phylogenetic analysis of Australian Triaenonychidae (Arachnida: Opiliones). - The aim of this study is to identify cladistic structure amongst Australian Triaenonychidae as a base for a wider study involving the entire family. The Triaenonychidae has a largely Gondwanan distribution with extensions into North America, Japan and Korea. It is not known from India.
A matrix of 42 genus level taxa and 35 characters was analysed using HENNIG86. Four well supported terminal clades were identified: those containing *Lomanella, Nunciella, Equitius* and the Triaenobuninae *sensu* Roewer. Further analysis suggests that the Triaenobuninae *sensu* Roewer is paraphyletic relative to the Triaenonychinae.
The status of the *Lomanella* clade as a possible new subfamily grouping is discussed. The analysis has to be widened to embrace the whole family across its entire distribution before more definite judgements on family level classification can be made. Analysis of a larger character set incorporating non-Australian genera is planned for a future study.

Key-words: Phylogeny - Analysis - Opiliones - Triaenonychidae - Australia.

INTRODUCTION

The first Australian genus and species belonging to the Triaenonychidae Soerensen 1886 were described by SIMON in 1880 from a series of specimens collected in the Blue Mountains, near Sydney. Since the description of *Equitius doriae*, over 130 additional species in about 40 Australian genera have been described, particularly from Tasmania. The relationships between Australian genera have remained obscure, although generally they have been regarded as falling into two major groups, the Triaenonychinae and Triaenobuninae (HICKMAN, 1958) (though FORSTER 1954 considered the groups to have only the status of Tribe within the Triaenonychinae).

Several attempts have been made to refine the family level classification of the Triaenonychidae: ROEWER (1915) focussed on sternal shape, FORSTER (1954), BRIGGS (1971) and SUZUKI (1975) on morphology of tarsal claws, and more recently MARTENS (1986) has suggested that male genitalic characters might be of more value in defining major groupings. The literature has been reviewed by HUNT & HICKMAN (1993).

No studies have attempted to resolve the issue of higher classification by the use of cladistic analysis. In this preliminary study, cladistic structure and character evolution are explored in the Australian fauna and some observations made on higher classification. The analysis will, in a later study, be widened to embrace the whole family across its entire distribution. More definite judgements on family level classification will have to await the results of this study.

The Triaenonychidae is regarded as the most primitive family in the suborder Laniatores, having retained a fully developed muscle in the shaft of the penis (MARTENS 1986). Its sister family, the Travuniidae, retains a modified muscle restricted to the base of the shaft, while other laniatorid groups have lost the muscle completely. The Triaenonychidae has a largely Gondwanan distribution with extensions into North America, Japan and Korea. It is not known from India.

METHODS

Terminology in general follows FORSTER (1954, Figures 1 and 3) and HUNT & MAURY (1993, Figure 1). The type species was used to code for each genus and where possible corroborated by other species. Some nominal genera known to be junior synonyms, for example *Conoculus* Forster 1949 (= *Yatala* Roewer 1942), were omitted though synonymy has yet to be formalised. The more familiar *Callimcus* Roewer 1931 was used, although it is evidently a junior synonym of *Parattahia* Roewer 1915. *Perthacantha* Roewer 1931 (= *Dingnpa* Forster 1952) was omitted because of lack of genital data. Species groups, for example in *Lomanella* Pocock 1903, were included.

Polarity of character states for cladistic analysis was determined by outgroup comparison. Two outgroups were chosen: *Speleonychia sengei*, described by BRIGGS (1974), from the Travuniidae, a probable sister taxon to the Triaenonychidae (MARTENS 1986); and *Larifuga calcarata* Lawrence, 1931 (redescribed by KAURI, 1961), from the Adaeinae, traditionally regarded as a different taxon from family level taxa in Australia (ROEWER 1915; LAWRENCE 1931; FORSTER 1954; HICKMAN 1958). Noting Martens' character evolution hypothesis for penis morphology (Martens 1986), the penis of *L. calcarata* was regarded as plesiomorphic in form, that of *S. sengei* highly apomorphic. Penis characters were evaluated accordingly.

The complete matrix including the 2 outgroups was of 44 genera and 35 characters (71 character states) (Table 1). Basic analysis used the mhennig* and bb* subroutines of HENNIG86, version 1.5 (FARRIS 1988). Supplementary analyses used the successive *weighting* and *nelsen* strict consensus subroutines.

The following analyses were undertaken:

1. **Complete data matrix.** This resulted in 540 equally parsimonious trees (99 with successive weighting). Analysis always placed the outgroups in the ingroup. This is

regarded as an artifact due to the combined effects of presumed homoplasy, group size and the exclusion from the analysis of characters which only define the out-groups. Elimination of the outgroups from the analysis resulted in fewer cladograms (Table 2). The nelsen consensus of the complete data, however, was very similar to that for data minus the outgroups.

2. **Complete data matrix minus the outgroups.** Rooting was in the hypothetical ancestor where each character was coded as a plesiomorphy, determined by compa-rison with the outgroup character states. Character 26 was ambiguous for *Notonuncia* and *Leionuncia* so the polarity was coded in 3 separate analyses as ?, 1 and 0. Intuitively, it was felt 1 was correct because the wing-like lateral projections from the stylus (Figures 65 and 83, HICKMAN 1958) could well have arisen by intimate fusion of the flanking plates with the stylus. The results of these analyses are summarised in Table 2.

3. **Successive weighting.** Analyses in (2) were re-run using successive weighting (Table 2).

4. **Nelsen consensus.** This was applied to each tree output file in (2) and (3).

5. **Selection of trees for CLADOS output.** As expected, the nelsen tree from the weighted data showed greater resolution of cladistic structure than the nelsen tree from the unweighted data. The relevant "weighted" nelsen tree was compared to the trees in the unweighted tree output file. A tree which closely corresponded in topo-logy was selected for CLADOS (NIXON 1992) output (Figure 2) and analysed.

OVERVIEW OF MORPHOLOGY

DORSAL BODY STRUCTURES

Only two dorsal body structures were used in analysis (characters 0 and 1). Eyemound structures like the presence of a spine or eyemound position relative to the anterior margin of the carapace were not scored. In an earlier analysis these appeared excessively subject to homoplasy and resulted in overflow in the number of trees. Characters which could be considered in future analyses include the extent of development of tergal area 1 and the strength of spines on tergal area 3. A promising character, but not yet understood because of insufficient data, is the pattern of fusion of tergites into the scute during development. Both *Lomanella* and *Nunciella* appear to differ from taxa like *Equitius* in their patterns of fusion.

VENTRAL BODY CHARACTERS

The classical family-level character of sternum shape was used in the analysis (characters 2 and 3). A wedge-shaped sternum with a narrow base, present in both outgroups, was regarded as plesiomorphic. There is potential for the recognition of

more subtle character states: sternal shape may vary in subtle ways correlated to the evolution of surrounding structures: mouthparts, coxae, architecture and position of genital opening, and penis size. For example, Hunt & Maury (1993) showed that shape can vary in cases where penises have hypertrophied. Nevertheless, Roewer's (1915) characterisation of sternum shape remains a good generalisation. Similarly, the position of the genital operculum (character 5) has potential for multistate coding. There seem to be gradations between an extreme anterior position, and the extreme posterior position in *Lomanella*. Any anteriad displacement is coded here as 1. Character 4 (whether the spiracle in exposed or covered) appears to be a important character and an ultrastructural study may yield further useful characters.

APPENDAGE CHARACTERS

Chelicera: other than the presence of a boss (character 12), no other characters were used. In an earlier analysis, the presence/absence of a prodistal spine on the basal article was used but found to be very homoplastic, generating many additional trees without clarification of structure.

Pedipalp: several characters, particularly relating to spination of the femur (characters 13-16) were used. Modification of the proximoventral spine is particularly useful.

Legs: characters relating to increase in the number of tarsal articles in both sexes (character 6) and the male (character 7) are useful but need to be evaluated with caution (Hunt, 1971; 1985). The presence of a ventral notch in the calcaneus of leg 1 in males of some taxa (character 8) is a very interesting character (see Results and Discussion below). Spination of the femur of leg 1 (characters 9 and 10) help define clades but homoplasy in character 9 should be suspected. The presence of a peltony-chium on legs 3 and 4 (character 11) has implications for family-level classification (Hunt & Hickman 1993).

GENITAL CHARACTERS

Penis: The potential importance of penis structure in classification was de-monstrated in the pioneering studies of Forster (1954) and Martens (1986). A large number of characters has been used (characters 17 to 32). Among the most important are the presence of a constriction at or just above the base of the shaft (character 17); the loss of the dorsolateral plate (character 19) and the number of superior setae on the ventral plates (character 23). Detailed evaluation of character evolution of penis structures is planned for a further paper (Hunt, in prep).

Ovipositor: The only character used is the presence/absence of bifurcate setae, presence being a synapomorphy for the *Lomanella* complex (character 33).

TABLE 1

Complete data matrix of Australian genera and outgroups.

	0	4	5	9	10	14	15	19	20	24	25	29	30	34
ANCESTOR	00000		00000		00000		00000		00000		00000		00000	
SPELSEN *Speleonychus sengei* Briggs	00000		1100?		01000		00?01		?0000		01000		01000	
LARCAL *Louauella calcarata* Lawrence	0000?		?1001		00000		00?00		?0000		00000		0000?	
LOMRAN *Louauella raniceps* group	00010		00000		00000		11?00		?0000		10000		10010	
LOMINSOL *Louauella insolentia* group	00010		00000		00000		11?00		?0000		10000		10010	
LOMEXIG *Louauella exigua* group	00010		00000		01000		11?00		?0000		10000		10010	
LOMPELT *Louauella peltonychium* group	00010		00000		01000		11?00		?0000		10000		10010	
EQUITIUS *Equitius* Simon	00011		10110		00010		00100		00000		00000		00000	
HOLCAV *Holouuncia cavernicola* group	00011		10110		00010		00100		00001		00010		00000	
HOLRECT *Holouuncia recta* group	00011		10100		00010		00100		00001		00010		00000	
PARANUN *Parauuncia* Roewer	00011		10110		000?0		00100		00000		00000		00000	
ODONTO *Odontonuncia* Hickman	00011		10100		00010		00100		00000		00000		00000	
HICKMAN *Hickmanoxyomma* Hunt	00011		10100		00010		00100		00000		00000		00000	
NGENC New genus C	00011		10110		00010		00100		00000		00000		00000	
NGEND New genus D	00011		10110		00010		00100		00000		00000		00000	
CLUNIELL *Cluniella* Forster	00011		10001		00000		00100		10000		0?000		00000	
MESTONIA *Mestonia* Hickman	00011		10000		00000		00?00		10020		00000		00000	
STYLO *Stylouuncia* Hickman	00011		10100		0000?		00100		00000		0?000		00000	
MONOXY '*Monoxyomma*' *rotundum* group	00011		11001		00000		00100		01000		00000		00000	
TASMANYX *Tasmanonyx* Hickman	00010		11000		00001		00100		01000		01000		00000	
PYENGAN *Pyeuganella* Hickman	00011		11000		00000		10100		?0000		00000		10000	
ALLONUN *Allouuncia* Hickman	00010		11000		00000		00100		01000		01000		00001	
ANKYLO *Aukylonuncia* Hickman	00010		10010		00000		00100		00000		00000		00100	
CALLIUNC *Calliuncus* Roewer	00010		10000		00101		00100		00000		01000		00000	
NUNCIELL *Nunciella* Roewer	00010		10000		00101		00100		01000		01000		00000	
NUNCIOID *Nuncioides* Hickman	00010		11000		00101		00100		01000		01000		00000	
BRYONUN *Bryouuncia* Hickman	00010		10010		00000		00100		00000		00000		00100	
YATALA *Yatala* Roewer	00011		10001		00001		00101		00000		00000		00000	
TRIAENOB *Triaeuobuuus* Soerensen	11111		10001		10000		00?11		10010		00000		01000	
DIPRISTES *Dipristes* Roewer	11111		10001		10000		00?11		10010		00000		01000	
GLYPTOB *Glyptobuuus* Roewer	01111		10000		00000		00000		10010		00100		01000	
HETERON *Heteronuncia* Roewer	01011		10001		00000		001?1		00000		00000		00000	
PHANEROB *Phanerobuuus* Roewer	00111		10001		00000		00??1		10010		00100		01000	
CHILOBUN *Chilobuuus* Hickman	00111		10001		00000		00000		10020		00000		00000	
RHYNCHOB *Rhyuchobuuus* Hickman	00111		10001		00000		00001		00010		00101		01000	
TASMANON *Tasmanonuncia* Hickman	00011		10001		00000		00001		00010		00101		01000	
EUBUNUS *Eubuuus* Hickman	00111		10001		00000		00000		10010		00100		01000	
MIOBUN *Miobuuus* Roewer	00111		10001		00000		00000		10020		00000		00000	
CHRESTOB *Chrestobunus* Roewer	00111		10001		00000		00000		10120		00000		00000	
THELBUN *Thelbunus* Hickman	00110		10100		00000		00000		10120		00000		00000	
PHOXOBUN *Phoxobunus* Hickman	00111		10001		00000		00011		00010		00000		01000	
ALLOBUN *Allobuuus* Hickman	00111		10001		00000		00000		10020		00000		0?000	
NUCINA *Nucina* Hickman	00010		10100		00000		00101		00000		01000		01000	
NOTONU *Notonuncia* Hickman	00010		11010		00100		0010?		00000		00?00		00001	
LEIONU *Leionuncia* Hickman	00010		11000		00100		0010?		00000		00?00		00000	

CHARACTER ANALYSIS

The following list summarises polarities for the 35 characters: (0) is plesio-morphic; (1) is apomorphic. Sources illustrating characters are given in parentheses.

Character 0: Eyemound without spine with side-branches (0); eyemound with spine with side-branches (Figure 573, FORSTER 1954) (1)

Character 1: Carapace without areas enclosed by granules (0); carapace with areas enclosed by granules (Figure 573, FORSTER 1954) (1)

Character 2: Sternum with narrow posterior margin (Figures 13 and 14, FORSTER 1954) (0); sternum with wide crescentic posterior margin (Figure 15, FORSTER 1954) (1).

Character 3: Sternum expanding from anterior to posterior between coxae III (Figure 14, FORSTER 1954) (0); sternum narrow between coxae III (Figures 13 and 15, FORSTER 1954) (1).

Character 4: Spiracle not obscured by coxa IV and bridging tubercles (Figure 4, HICKMAN 1958) (0); at least partly obscured by coxa IV and bridging tubercles (Figure 1, FORSTER 1954) (1).

Character 5: Genital operculum in posterior position (Figure 9B, HUNT & HICKMAN 1993) (0); displaced to more anterior position (Figure 4A, HUNT 1992) (1).

Character 6: Both sexes with 3 articles in tarsus 1 (0); both sexes with equal numbers but >3 articles in tarsus 1 (1).

Character 7: Male and female with equal numbers of articles in tarsus 1 (0); male with more articles than female (1).

Character 8: Calcaneus of leg 1 of male without a ventral notch (0); with notch (Figure 13, HUNT 1985) (1).

Character 9: Ventral tubercles/spines on femur 1 not appreciably longer than those on dorsal surface (Figure 152, HICKMAN 1958) (0); appreciably longer (Figure 218, HICKMAN 1958) (1).

Character 10: Femur of leg 1 without both dorsal and ventral spines (0); with well developed dorsal and ventral spines (Figure 178, HICKMAN 1958) (1).

Character 11: Tarsus of leg 3 or 4 without peltonychium (Figure 3A, HUNT & HICKMAN, 1993) (0); with peltonychium (Figure 3C-G; HUNT & HICKMAN, 1958) (1).

Character 12: Basal segment of chelicera without proximodorsal boss (0); with proximodorsal boss (Figure 113, HICKMAN 1958) (1).

Character 13: Proximoventral spine on pedipalp femur without proximal accessory branch/setal base with distad to prolaterad orientation (0); with proximal accessory branch/setal base with distad to prolaterad orientation (Figure 1D,H, HUNT 1985) (1).

Character 14: Proximoventral spine on pedipalp femur of male not terminally axe-shaped or subequally bifid (0); terminally axe-shaped (in male) or subequally bifid (usually in female) (Figure 102, HICKMAN 1958) (1).

Character 15: Dorsal surface of pedipalp femur with spines (0); spines absent (Figure 1, bottom, HUNT & HICKMAN 1993) (1).

Character 16: Spines on pedipalp with long spinous base and relatively short seta (Figure 1, top, HUNT & HICKMAN 1993) (0); with short tubercular base and relatively long seta (Figure 1, bottom, HUNT & HICKMAN 1993) (1).

Character 17: Penis shaft without proximal or subproximal constriction for penis sheaths (Figure 1B, Hunt and Maury, 1993) (0) with proximal or subproximal constriction (Figure 1A, HUNT & MAURY 1993) (1).

Character 18: Penis shaft without long taper towards base (Figure 1B, HUNT & MAURY 1993) (0); with long taper (Figure 1D, HUNT & MAURY 1993) (1).

Character 19: Dorsolateral plates of penis present (Figure 1A, HUNT & MAURY 1993) (0); absent (Figure 1B, HUNT & MAURY 1993) (1).

Character 20: Ventral plates of penis showing some separation (Figure 4, FORSTER 1954)(0); completely fused (Figure 3A, HUNT 1995a) (1).

Character 21: Ventral plate lobes of penis bearing superior seta(e) close (Figure 4, FORSTER 1954) (0); widely separated Figures 1 and 4, HUNT 1971) (1).

Character 22: Ventral plate with setose superior setae (Figure 3E, HUNT 1995a) (0); with strap-like superior setae (Figure 3F, HUNT 1995a) (1).

Character 23: Ventral plates each with 1 superior seta (Figure 4, FORSTER 1954) (0); each with 2 superior setae (1); ventral plates each with 3 superior setae (2).

Character 24: Ventral plate sloping continuously from proximal to distal (Figure 5C, HUNT 1990) (0); with proximad concavity (Figure 3K, HUNT 1992) (1).

Character 25: Ventral plate not intimately fused with stylus (Figure 2a,b, MARTENS 1986) (0); intimately fused with stylus (Figure 2c, MARTENS 1986) (1).

Character 26: Stylus of penis not closely enveloped by plates (Figure 123 and 124, HICKMAN 1958) (0); closely enveloped by plates (Figures 1-5, HUNT 1971) (1).

Character 27: Stylus subdistally without mediodistal spine (Figure 1A, HUNT & MAURY 1993) (0); with mediodistal spine (Figure 1B, HUNT & MAURY 1993) (1).

Character 28: Stylus of penis subdistally without denticles (0); with denticles (Figure 4,G-H, HUNT 1992) (1).

Character 29: Stylus of penis without prominent ventral lobe (Figure 4A, HUNT & MAURY 1993 (0); with prominent ventral lobe (Figure 4C, HUNT & MAURY 1993) (1).

Character 30: Dorsal plate present (Figure 1A, HUNT & MAURY 1993) (0); absent (Figure 1E, HUNT & MAURY 1993) (1).

Character 31: Dorsal plate proximally not bent sharply ventrad (Figure 1A, HUNT & MAURY 1993) (0); bent sharply ventrad (Figure 1B, HUNT & MAURY 1993) (1).

Character 32: Penis without mid-dorsal large spiny lobe (Figure 90, HICKMAN 1958) (0); with large spiny lobe (Figure 13, HICKMAN 1958) (1).

Character 33: Setae of ovipositor without proximal accessory branch (Figure 2C, HUNT 1995a) (0); with proximal accessory branch (Figure 5H, HUNT & HICKMAN 1993) (1).

Character 34: Smooth area of coxa III next to sternum not with mounds formed by enlarged setal bases (0); with mounds formed by enlarged setal bases (1).

RESULTS AND DISCUSSION

Basic tree calculation data are given in Table 2. The nelsen consensus of 27 trees produced by successive weighting with polarity of 1 for character 26 in *Notonuncia* and *Leionuncia* is shown in Figure 1. It contains a high level of cladistic structure and is identical to the nelsen tree from unweighted data, except that there is greater resolution in the clade at node 50 (Inset A, Figure 1, shows the corresponding clade from unweighted data).

TABLE 2

Basic data on tree calculations for 42 Australian genera and 35 characters, rooting in Ancestor.

Coding of Char. 26 in *Notonuncia* & *Leionuncia*	Weighting	Tree length	ci	ri	No. of trees
?	none	66	54	83	252
	Successive	280	78	92	45
1	none	67	53	82	96
	Successive	280	78	93	27
0	none	66	54	83	144
	Successive	280	78	92	27

Figure 2 is a CLADOS output of one of the 96 trees in the unweighted output. This tree was chosen because it most closely corresponded to the nelsen tree of Figure 1, and served as the basis for the following analysis of results.

Two clades occur at the base of the cladogram, at nodes 69 and 70 (Figure 2). The major clade is supported by 1 strong synapomorphy in character 5. Character 17 is not regarded as strong as it was coded ? for the members of the minor clade at node 69 and requires a major reversal at node 50.

At the next highest level in the cladogram there is an unresolved trichotomy. The clade at node 68 is supported by a homoplasy, namely sexual dimorphism in the number of articles in the tarsus of leg 1. Interestingly, *Nucina* has been placed in this clade. This genus has a highly derived penis structure (Figure 28, HUNT & HICKMAN (1993)) which shows some convergence with the clade at node 69. Its separate affinities from *Lomanella* (node 69) were emphasised by HUNT & HICKMAN. While further analysis may challenge the monophyly of the clades at nodes 68 and 64, the clade at node 61 is almost certainly monophyletic.

I suspect that as our knowledge of the family increases the clade at node 66 may prove polyphyletic, being based on a potentially very homoplastic character: a non-sexually dimorphic increase in the number of segments in the tarsus of leg 1 (for example, increase in number is often a consequence of cave adaptation and is possibly susceptible to other selection pressures). Support of node 66 by this character also required reversals at nodes 51 and 55.
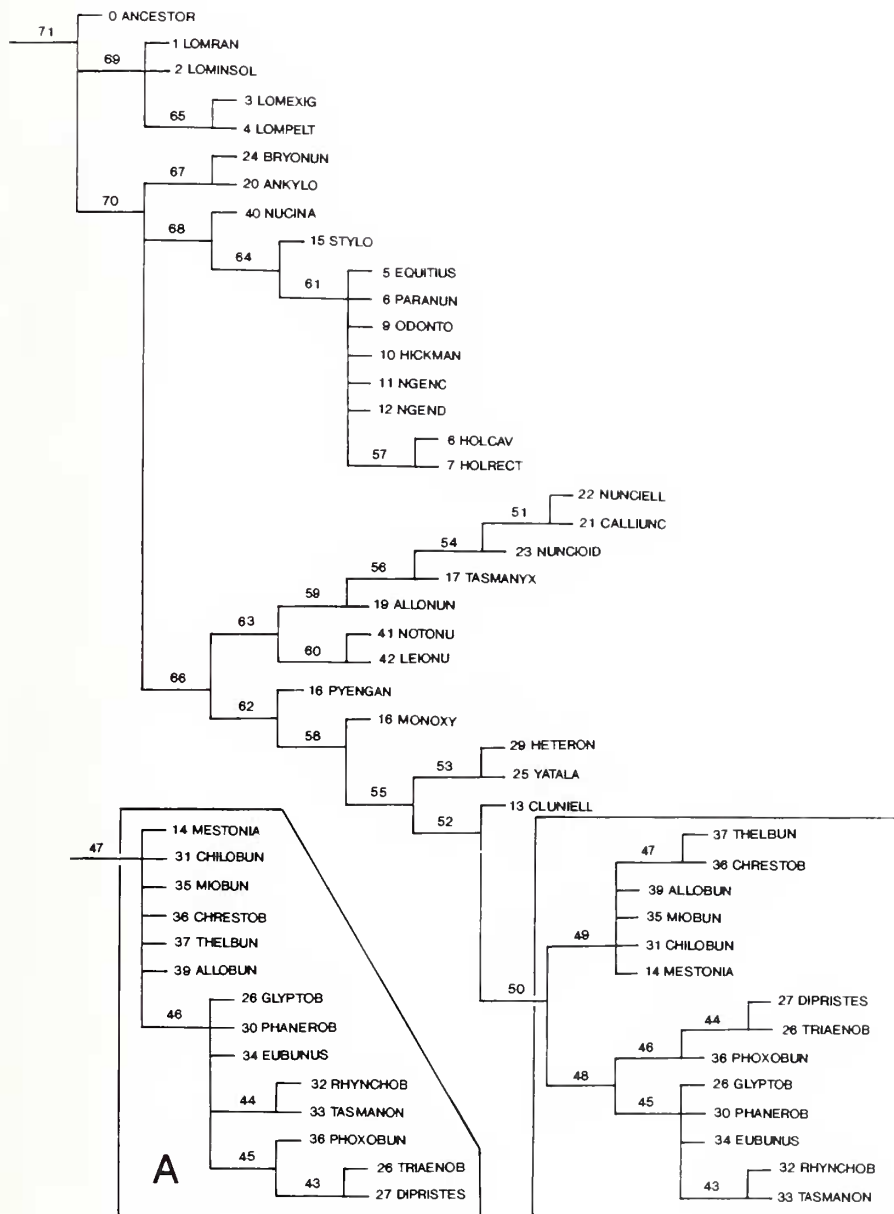
FIG. 1

Nelsen consensus of 27 trees produced from successively weighted data, coding of Character 26 for *Notonuncia* and *Leionuncia* set at 1. **Inset A:** The part of the nelsen consensus of 96 trees produced from unweighted data which differed from the consensus from weighted data. Full taxa names for abbreviations given in Table 1.
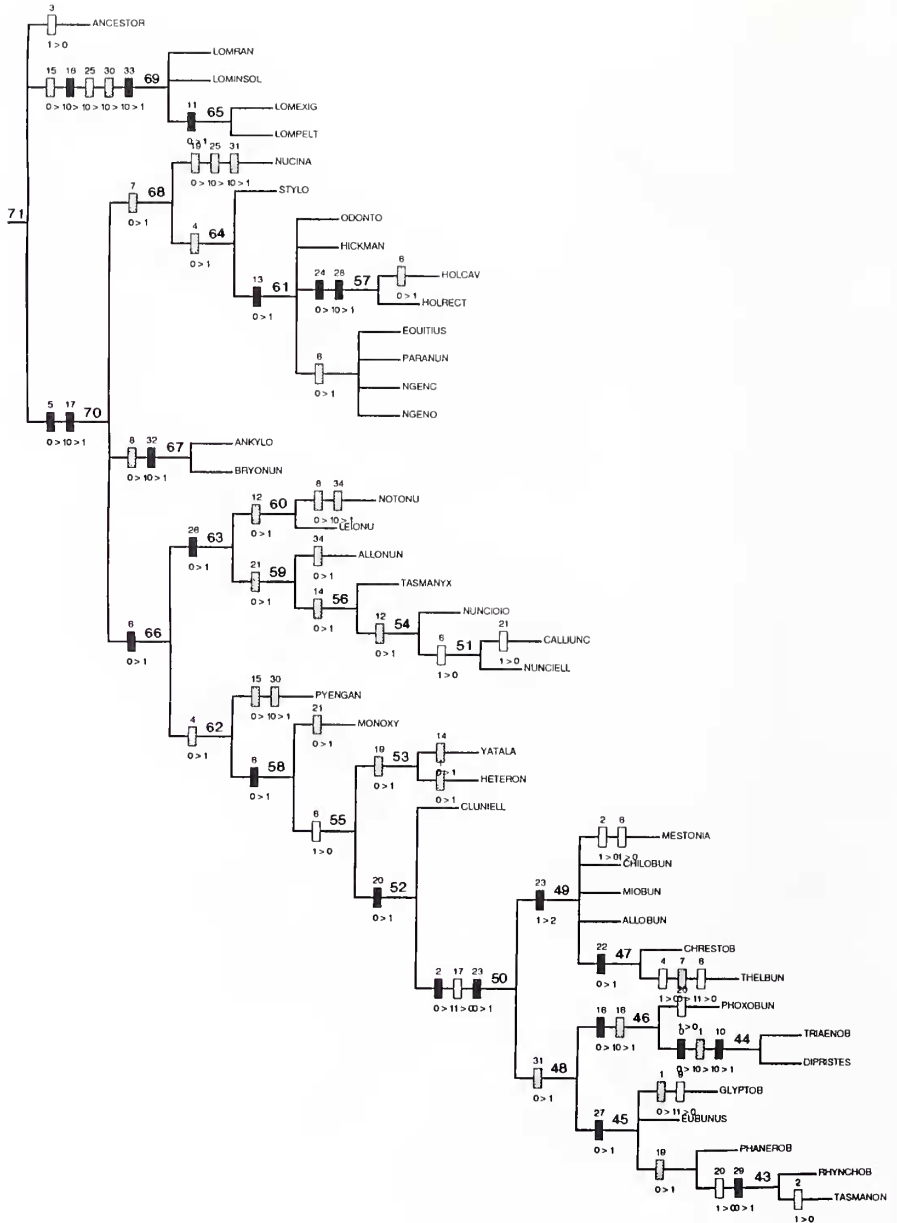
FIG. 2

CLADOS plot of a tree, selected from 96 trees produced from unweighted data, which corresponded most closely in topology with the NELSEN consensus in Figure 1 produced from successively weighted data. Black bars = synapomorphies; stippled bars = homoplasies; white bars = reversals. Full taxa names for abbreviations given in Table 1. Nodes numbered to correspond to nodes in Figure 1.
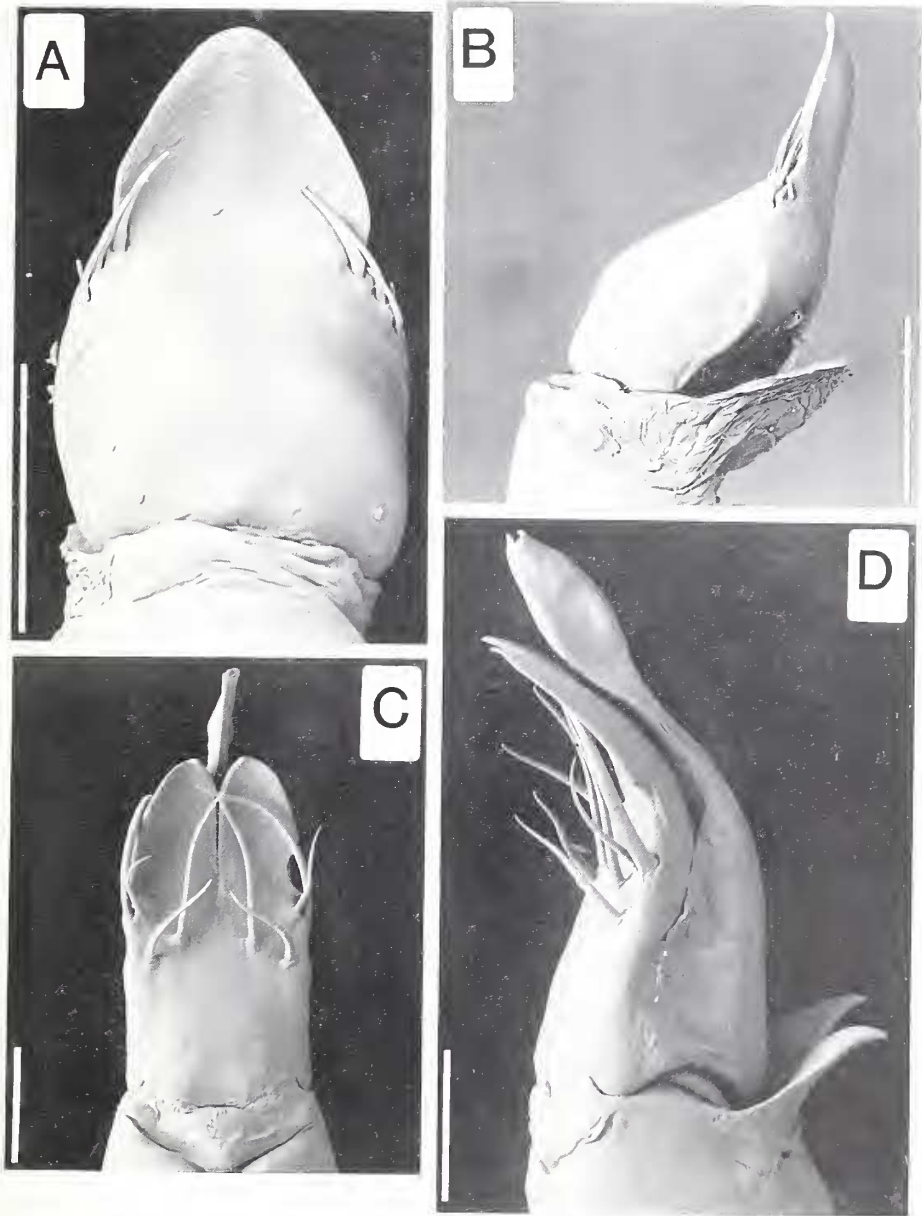
Fig. 3

Terminal part of penis of *Lomanella raniceps* Pocock (A,B), and of *Pyenganella striata* Hickman (C,D). A,C ventral; B,D lateral. Scale bars: A,B = 100μ ; C,D = 200μ .

The clade at node 67 may well come to lie with the clade at node 60: there is considerable similarity between the constituent genera in the shape of the ventral plate of the penis and the disposition of inferior setae, characters which have not been coded for this analysis. When character 26 was coded as ? or 0, *Notouuucia* plus *Leiouuncia* fell into the polytomy at the same level as *Bryonuncia* plus *Ankylouuucia*.

The clade at node 54 is almost certainly monophyletic. It is interesting that its sister genus is *Tasmanonyx* Hickman, suggested by HICKMAN (1958) as possibly belonging in the Soerensellinae, a predominantly New Zealand group (FORSTER 1954). It is possible that its placement in clade 63 in based on homoplasies and that a broader analysis including the Soerensellinae would force a change of position on the cladogram.

The clade at node 50 is the Triaenobuninae, one of the 3 subfamilies erected by ROEWER (1915) on the basis of sternal structure. The analysis has placed two genera, formerly placed in the Triaenonychinae by HICKMAN (1958), in the "triaenobunine" clade. These are *Mestonia* Hickman and *Tasmanouuucia* Hickman. Their placement respectively in clades 49 and 45 seems secure.

Comments on character 8

The distribution of character 8 (presence of a ventral notch in calcaneus 1) is of interest as it appears to have arisen independently in at least 2 clades in Australia, that containing *Equitius* and that containing *Notouuncia* (the clade containing *Ankylonuncia* which also has character 8 will probably be shown to belong with *Notonuncia*).

The notch is involved in mating, helping to brace the male against the female (HUNT 1979). It also occurs in taxa in South Africa, Madagascar and South America (LAWRENCE 1931; 1959; KAURI 1961; MAURY 1990), though apparently not in New Zealand (FORSTER 1954). It will be interesting to see whether, in a wider analysis, the character has arisen independently in several taxa or whether these taxa are more closely related than appears at present to be the case.

Despite its use in mating, it may be a plastic character, capable of being switched on or off during development. The *Holouuucia recta* group does not have a notch though the *Holouuncia caveruicola* group does. Both are clearly closely related (Figure 2). Similarly *Leiouuucia* is very similar to *Notouuucia* but lacks a notch. *Odoutouuucia* appears to be a "notchless" *Paranuucia*.

Comments on subfamily classification of the Triaenonychidae

The Triaenobuninae *sensu* ROEWER (1915) seems to form a clade (above node 50, Figure 2) within the Australian fauna though it is paraphyletic relative to taxa in the Triaenonychinae *sensu* ROEWER. Nodes 62, 58, 55 and 52, however, are supported by weak characters and it is possible that an analysis involving a larger number of characters, and genera from outside Australia, will resolve the Triaenobuninae as a separate monophyletic group relative to the Triaenonychinae. Its present paraphyletic
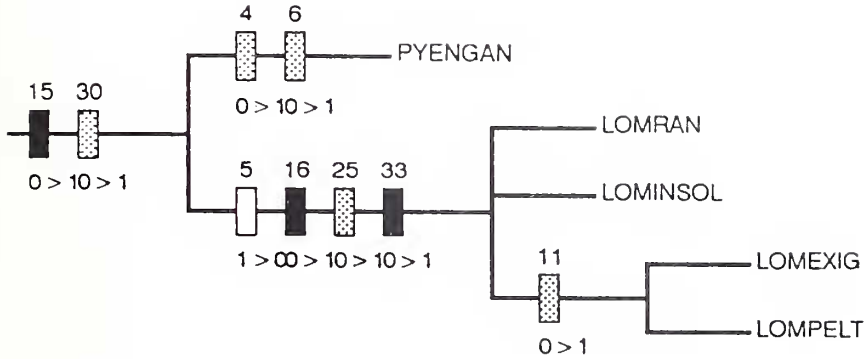
FIG. 4

Hypothetical branch of cladogram showing *Lomanella* + *Pyenganella* as a terminal clade. Full taxa names for abbreviations given in Table 1.

position, however, adds force to FORSTER's (1954) belief that the subfamily Triaeno-nychinae should encompass the triaenobunine taxa (though Forster still recognised the Triaenobunini as a tribe). Debate on family level classification was rekindled by BRIGGS (1971) and more recently reviewed by HUNT & HICKMAN (1993).

The *Lomanella* taxa of clade 69 were conservatively regarded by HUNT & HICKMAN (1993) as belonging to a single genus. However, I now believe that at least 3 generic groupings could be justified. If this clade were to maintain its basal monophyly in a family-wide analysis, then elevation of the clade to subfamily status may be appropriate.

With further study, the *Lomanella* clade may more properly be regarded as a terminal taxon supported by strong synapomorphies, possibly including neotenic reversals. In this regard, it is interesting that the genus *Pyenganella* HICKMAN could possess a primitive form of the *Lomanella* penis: the dorsolateral plates are orientated in a similar way, the dorsal plate has been lost, and the stylus of the *Pyenganella* penis is intimately associated with the ventral plates but apparently not yet fused with them (Figure 3, see also the penis of *L. revelata*, Figure 17 H-J, HUNT & HICKMAN (1993)). A hypothetical cladogram showing possible character evolution with *Lomanella* and *Pyenganella* belonging to a terminal clade is given in Figure 4.

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